Bird Composition as an Ecological Indicator of Forest Disturbance Levels

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Abstract

Ecological indicators are needed to evaluate natural biodiversity and to estimate environmental change. I used bird community composition as an environmental indicator to evaluate forest disturbance (at the community level) in areas of Western Mexico. Surveyed bird and vegetation composition data at 79 sites within regions of the Sierra Madre del Sur and Transvolcanic Belt Provinces of Central Mexico were used. Bird species were classified into four habitat assemblages (groupings) according to their habitat preference (the habitat characteristic for their presence). Birds found primarily in late successional forests are sensitive to forest disturbance and a predominant presence of these species would indicate an undisturbed mature forest habitat. Birds tolerant to forest disturbance are characteristic of early-successional, clearcut, brushy and fragmented landscapes. Presence of predominately disturbance tolerant species would suggest a disturbed habitat. The number of species in each habitat assemblage were counted for each site and used to calculate bird community index values. The bird community index provides a value to assess the habitat disturbance on bird communities. Bird species were also classified into nesting, foraging and feeding guilds.

In order to evaluate the relationship between individual species response and responses of other species of that same functional group, correlation coefficients between

the presence or absence of each individual species and the number of co-occurring species from the same functional group or habitat assemblage were calculated. Binary logistic regressions were used to predict the probability of occurrence (for the dominant 4 co-occurring birds within each functional group and habitat assemblage) relative to percent canopy cover. Correlations between functional group species richness and average percent canopy cover and average stand basal area were calculated. Habitat assemblage species richness and total species richness for each site were also correlated to those same values.

Bird communities on the majority of the surveyed areas were dominated by disturbance sensitive species. Only one site was dominated by disturbance tolerant species. Habitat assemblage and guild members showed internal cohesion (consistent responses to different disturbance levels) but did not show strong correlations to the canopy cover and basal area. The probability of occurrence versus canopy cover for the four top birds in each guild and habitat did not show consistent trends, indicating different responses toward vegetation metrics within the grouped species. The bird community index also did not show strong correlations to the percent cover and basal area, suggesting that the index should not be used independently in assessing bird community and forest condition.

Because data on forestry and avian communities in Mexico are not readily available, bird community surveys could still serve as a good tool for assessing forest condition at the community level in this region.

Introduction

An ongoing topic of interest for conservation biologists is how to effectively monitor ecosystem biodiversity as well as how to most accurately estimate environmental changes (Hawksworth 1995). Because ecosystems are so intricate, the ability to measure all the components of diversity is an overwhelming, if not an impossible task. Direct documentation of ecosystem changes is both cost and time intensive (Mikusiński and Angelstam 1997) therefore use of ecological indicators is a more pragmatic approach to efficient monitoring. Ecological indicators allow ecosystems to be described in simpler terms and can be used to reflect a variety of different ecological aspects. Although development and selection of ecological indicators is a complicated process, the resulting information gained about the current state of the environment 1) permits evaluation of environmental policies, 2) can be used to identify environmental trends, 3) can be utilized by policy decision makers and 4) allows environmental biologists to study relationships between anthropogenic disturbances (due to changing landscapes and land use) and the environment.

The use of ecological indicators does have limitations however. Although indicator species have been used in practical management of biodiversity at the local, regional, national and international levels (Bibby et al. 1992; Margules et al. 1994), the availability of data and information is often hard to obtain. Other limitations include: lack of an across-level standard methodology, subjectivity in rankings of indicators and the lack of reference levels which makes it difficult to identify overall changes.

Monitoring ecosystems can be carried out by using an individual species as an ecological indicator. Individual species have been used for decades as a convenient assay of environmental conditions (Thomas 1972; Zonneveld 1983). Species that are used as ecological indicators are done so under the assumption that the response of that individual species characterizes current habitat conditions and/or is representative of the responses of other species within that same habitat or community (Canterbury et al. 2000). In other words, indicator species are assumed to signify the status of the environment and/or serve as proxies for a larger number of species (Block et al. 1986; Furness & Greenwood 1993) which can then provide information on measurements of biodiversity condition and transformation (Hawksworth 1995; Morrison et al. 1992; Noss 1990). Plant and invertebrate species have been effectively used as ecological indicators to evaluate the change in the quality of air and water (Ott 1978; Phillips 1980; Newman & Schreiber 1984) due to agricultural and range land practices (Clements 1920; Stoddart et al. 1975).

Criticisms pertaining to the use of individual species as ecological indicators have been brought forth. A major argument against the use of individual species as indicators is that the individual species may not necessarily represent the other species occurring in that same habitat. Co-occurring species may prefer a dissimilar niche, they may have different life histories and they may react independently to environment changes (Landres et al, 1988; Lindenmeyer 1999; Morrison 1986; Niemi et al. 1997; Weaver 1995).

Individual species have been used as indicators for analysis within a restricted part of the community. For example, one could use an individual species to assess the abundance of other species belonging to the same *guild* (Severinghaus 1981). A guild is defined as “a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). This however, still assumes that individual species within a guild all respond in similar ways to environmental changes. As stated previously, since co-occurring species may require different environmental conditions, the occurrence of an individual species may provide only modest information on overall guild abundance or diversity.

Ecological indicators based on species frequency occurrence (belonging to the same guild) are also problematic (Verner 1984) because large spikes in the population number of just a few species can mask the decrease or loss of other species in that same guild (Mannan et al 1984). Guilds are useful in analyzing collective responses of different species to changes in the ecological condition and resources that define that particular guild. Therefore, in order for a guild to be effectively used as an ecological indicator, population responses among species of the same guild must be consistent and the definition of the guild must be carefully defined.

Criteria that have traditionally been used to define guilds include foraging techniques, nesting locations as well as diet and habitat preferences (Root 1967; Wilson 1974; Szaro 1986). For the purposes of this project, bird species will be categorized into functional groups based on the above mentioned four criteria and will then be used as indicators for assessing the relationship between bird communities and forest disturbance.

"Habitat" for this project is defined simply as the vegetation structure – what types of vegetation is present - and does not encompass physical, chemical or biological factors in the environment. Additionally, habitat preference is not actually a "guild" according to the definition given by Root because there is no exploitation of a specific ecological resource. Therefore, habitat preference categories will be referred to henceforth as habitat “assemblages.”

Habitat assemblages are defined by successional habitat preferences (Croonquist & Brooks 1991). In comparing correlations between habitat assemblage and other guild responses to species abundance, it has been shown that the former results in higher correlations (Szaro 1986). Since habitat assemblages are defined only for a certain habitat and therefore source condition, a combination of multiple habitat assemblages is necessary in order to obtain a more qualified and broad based assessment of the current condition.

Through this project, I will use forest bird composition to estimate forest disturbance levels using generated bird community index values over a broad region of Western Mexico. I will then look at how suitable the bird community index is in estimating forest disturbance by assessing 1) the consistency of bird population responses among functional group members, 2) the consistency of bird species responses to vegetation within functional groups and 3) the relationship between bird species richness of each functional group and habitat assemblage to vegetation measures.

Methods

Study Area

Bird censuses and vegetation surveys were conducted by L. González Guzmán across 79 sites in Western Mexico during the period of November 18 1996 and March 11 1997. Sites were distributed across areas of the Sierra Madre del Sur and Transvolcanic Belt Provinces of Central Mexico and included forested regions within the states of

Nayarit, Jalisco, Colima, Michoacán, Estado de Mexico, Morelos and Guerrero. Forest types included in the surveys were cloud, coniferous, oak, coniferous-oak, semi-deciduous and deciduous forests.

Bird and Vegetation Surveys

Bird censuses were conducted for each site using the fixed-point method developed by Hutto et al. (1986) and census routes followed available trails. Each site was sampled during one day and censuses began 30 minutes after sunrise. A single site census consisted of 10 separate point counts, separated by 200m intervals. The duration of each point count was 10 minutes and all birds observed within a 25m radius were recorded. Multiple repeat surveys at each site were not conducted due to the need to maximize the number of sites and to sufficiently survey a large geographic region. However, the fixed-point method and count duration applied at each point is usually adequate to maximize the number of bird species identified during one survey (Petit et al, 1995).

Vegetation data was also collected at each bird point count location. All tree species observed within a 20m diameter plot were recorded in addition to measurements of individual tree percent canopy cover and diameter at breast height.

Bird classifications

After identification, birds were classified into four habitat assemblages (Appendix 1) according to habitat preference for that individual species. Habitat preference is the habitat characteristic for the presence of an individual species. Birds placed into the mature forest assemblage (MF) are sensitive to forest disturbance and their presence is characteristic of late-successional forests. Birds tolerant to forest disturbance were placed into either the shrubland assemblage (SL) or forest edge assemblage (FE). Birds designated to SL are characteristic of early-successional clearcut and brushy habitats while those designated to FE are most commonly found in fragmented landscapes, suburbs and agricultural lands. Birds that could not be classified into a single assemblage, due to overlapping habitats, were classified as neutral species and were placed into the generalist assemblage (GEN). Habitat preferences for individual bird species were designated using literature cited data (IUCN 2004) and not the observed survey data, to avoid circularity of inference.

Bird species were also classified into diet, foraging and nesting guilds using literature cited data (Howell & Webb 1995). The diet guild included insectivore, granivore/herbivore, omnivore and nectarivore functional groups. The foraging guild was comprised of flower, bark, aerial, ground and foliage-foraging functional groups and the nesting guild consisted of ground, cavity, building, canopy (tree branch) and shrub-nesting functional groups.

Data Analysis

The number of mature forest, shrubland, forest edge and generalist bird species observed at each site were counted and used in the BCI formula: $\ln(MF + 1) - \ln(SL + FE + 1)$ to calculate the bird community index value for that particular site. This BCI formula was developed by Canterbury et al. (2000) and contrasts disturbance-sensitive (MF) species to disturbance-tolerant (SL and FE) species. A positive bird community index value suggests a bird community comprised mainly by disturbance-sensitive species whereas a negative bird community index value indicates a community where disturbance-tolerant species dominate.

Correlation coefficients between the presence or absence of each individual species at each site and the number of co-occurring species from the same functional group or habitat assemblage were calculated across all sites in order to assess the relationship between individual species response and responses of other species of that same functional group. Resulting values were shown through stacked histograms. Groups comprised of a single species were excluded because the number of other species in that group was zero. Correlation distributions centered around zero indicate independent assortment of species within a group. Predominately positive correlation values however, indicate internal cohesion within a group, suggesting that members of the group share similar responses to environmental conditions. A Monte Carlo simulation generator (10,000 replicates) was used to calculate a one-tailed *p* value.

Individual tree DBH (diameter at breast height) data was used in the formula: $\pi*(DBH/2)^2$ to calculate individual tree BA (basal area). Individual BA values were combined and used to compute the SBA (stand basal area = individual BA total/point area) for each point (n = 790). SBA values for each point were then averaged for each site (n = 79). Percent canopy cover values were averaged for each site also. Averaged SBA and percent canopy cover were used to characterize the habitat at each bird sampling site.

Individual bird species response to canopy cover was assessed through the use of binary logistic regressions. For each functional group and habitat assemblage, bird species were ranked based on the number of sites where each species was observed. For example, a species observed at ten sites was ranked higher than another species that was observed at five sites. The four most commonly occurring birds in each functional group and habitat assemblage were then selected. An occurrence metric (1 = present; 0 = not present) for each of the birds was generated, indicating presence or absence of each bird of interest at each site. The species occurrence metric at each site was then plotted against average percent canopy cover, across all sites. Binary logistic regression analysis via Minitab statistical software was used to generate regression equations that predict the probability of occurrence (for the four most commonly occurring birds within each functional group and habitat assemblage) relative to percent canopy cover.

To assess whether guild and habitat assemblage species richness can be explained by differences in vegetation, I correlated species richness of each functional group to the average percent canopy cover and the average stand basal area at each site. Species richness of each habitat assemblage and total species richness for each site was also correlated to both average percent canopy cover and average stand basal area.

Results

Correlation of variation within the functional groups

Mean correlation values between individual species and the number of other species of the same functional group were significantly greater than zero ($p < 0.001$) for canopy nesters (mean $r = 0.05$), ground nesters (mean $r = 0.04$) and shrub nesters (mean $r = 0.07$), but not significantly positive for cavity nesters (Figure 1a). Predominately positive correlations indicate internal cohesiveness within the community, suggesting that the group of species share similar population responses to the range of environmental variation sampled. Mean correlations for diet guilds (Figure 1b) were significantly greater than zero for nectar feeders (mean $r = 0.11$), omnivore feeders (mean $r = 0.05$) and insect feeders (mean $r = 0.04$), although they were not significantly positive for seed feeders. Mean correlations for all functional groups of the foraging guild (Figure 1c) were significantly greater than zero: foliage foraging (mean $r = 0.03$), aerial foraging (mean $r = 0.03$), flower foraging (mean $r = 0.08$), ground foraging (mean $r = 0.08$) and bark foraging (mean $r = 0.17$). Mean correlations were significantly greater than zero for the generalist (mean $r = 0.03$) and mature forest (mean $r = 0.03$) assemblages, but was not significantly positive for the shrubland and forest edge assemblage (Figure 1d).

All histograms are right-skewed and all functional groups, except the bark foraging functional group, contained at least five species that were negatively correlated with the species richness of other functional group members. Species having the highest positive correlations belonged to the canopy nesters, nectar feeders and flower foraging functional groups. The building nesters functional group contained only one species and was therefore excluded from the data set.

<u>Consistency of species responses to canopy cover within functional groups</u>

To examine responses of individual species to canopy cover, I examined the probability of occurrence for the four most abundant bird species in each assemblage and guild with respect to percent canopy cover.

Examination for the four most common occurring species in each habitat assemblage did not show resulting consistent trends (Figure 2). The forest edge assemblage did not show consistent responses. Three of the four birds increased with increasing canopy cover. One of the increasing probability species showed the steepest increase at approximately 10 percent canopy cover while the remaining fourth bird species showed a decrease with increasing canopy cover. In the generalist habitat assemblage, three of the four bird species decreased with canopy cover and one bird species showed an increase in probability, albeit at a flattened rate. All four species had a high probability of occurrence at low canopy cover levels however. The mature forest and shrubland assemblages also did not show consistent trends either. In the mature forest assemblage, two species increased steadily with increasing canopy cover, one species increased sharply and conversely, one species decreased steeply. In the shrubland habitat assemblage, two species (whose probability of occurrence was low at low canopy cover) increased with increasing canopy cover while one species probability dropped dramatically beyond canopy cover of 5% and another did not change considerably.

Analysis of the four nesting guilds (Figure 3) showed that in the cavity nesting guild, probability of occurrence for two bird species increased, while two others decreased. In the canopy nesting guild, three species increased with similar curves and the occurrence probability of one species decreased with canopy cover. The ground nesting guild showed two species with rather flattened probabilities and of the remaining two species, one increased and the other decreased steeply. The shrub nesting guild showed three species decreasing with canopy cover and one species increasing.

Of the four diet guilds, none showed consistent responses for occurrence probability (Figure 4). In the insect feeding guild, two species increased and two others decreased with increasing canopy cover. The nectar feeding guild showed that three species increased and one decreased, while the opposite was seen for the omnivore guild. The seed feeding guild had increased occurrences for three of bird species.

The five foraging guilds did not show consistent trends for response in all four constituent species (Figure 5). In both the flower and aerial foraging guilds, three species' probabilities of occurrence increased. The two bark foraging species showed different responses also – one increased and one remained close to zero. The foliage foraging guild showed two species with increased and two species with decreased probabilities and the ground foraging guild depicted three decreased species probabilities and one species with an increased probability with increasing canopy cover.

Of all the guilds and assemblages, none showed similar responses for all four analyzed bird species. Assemblages and guilds that showed three of the four birds with similar responses included the forest edge, generalist and mature forest assemblages as well as the canopy nesters, shrub nesters, nectar feeders, omnivores, seed feeders, flower foraging and ground foraging guilds The generalist assemblage, canopy nester guild and shrub nester guild showed the most similar responses to canopy cover within those three species.

Correlations between functional groups and vegetation measures

Average percent canopy cover and average stand basal area were significantly intercorrelated ($r = 0.47$; $p < 0.001$) but resulting correlation values between functional groups and the vegetation measures - though significant ($p < 0.001$) - showed some variation (Table 1).

The vegetation measure associated with the largest correlation values overall were found between functional group species richness and average percent canopy cover. The shrub nesters functional group had the strongest correlation ($r = -0.26$), followed by the insectivores functional group (r = -0.20). Otherwise, the diet and nesting guilds had generally weak correlations to average percent canopy cover. The correlation values for the foraging guild groups were more consistent than those of the diet and nesting guild. The foliage foraging group had the strongest response in the guild (r = -0.14). Of the habitat assemblages, the generalist assemblage had the strongest response (r = -0.19).

Functional group correlations with average stand basal areas were generally weaker compared to average percent canopy cover. The shrub nesters and aerial foraging groups had the strongest correlations to average stand basal area (r = -0.14) and though the diet guild reflect low correlations, the nectarivores group had the strongest response within that guild (r = -0.09). The aerial foraging and shrub nesters had the strongest correlation values in their respective guilds (r = -0.14) and forest edge had strongest response (r = -0.19) out of the habitat assemblages.

The bird community index produced by combining shrubland, forest edge and mature forest assemblages did not show stronger correlations with the vegetation measures when compared to those of individual assemblages. When correlated with average stand basal area, the bird community index actually had one of the lowest values (r = 0.01). Additionally, total species richness was weakly correlated with the vegetation measures.

Analysis of bird community index

Seventy eight out of the seventy nine surveyed sites had positive bird community index values. This indicated that the habitat assemblage that dominated bird communities in the surveyed sites was the mature forest assemblage. Bird communities therefore, are suggested to be dominated by disturbance sensitive species.

Consequently, if the boundary between undisturbed and disturbed bird communities is defined by an index value of zero, which would represent equal numbers of disturbance tolerant and disturbance sensitive species (Canterbury et al. 2000), only 1% of the sites would be classified as disturbed.

Discussion

The results of this study show that in the surveyed regions of western Mexico, based on the bird community index values, the vast majority of sites could be classified as undisturbed. Ninety-nine percent of the sites had a positive bird community index value indicating bird communities that were dominated by disturbance sensitive species. Disturbance sensitive species presence is characteristic of mature forest and late-successional habitats. These results can be supported because the original data collector attempted to select sites that were not highly populated.

The bird community index however, provides only a general-based indication on the degree of forest disturbance on bird communities (Canterbury et al. 2000) and in this study, did not show a strong correlation to vegetation measures (Table 1). Although the index enlists the use of multiple habitats, the bird community index should not be used independently, uncritically or without caution. One reason is because single species status can be masked by the overall trend in the guilds that the species is a member of. This is especially important when the species is listed as threatened or endangered – a situation that in all probability warrants a different monitoring procedure. The bird community index provides a simplified picture of an environment by consolidating multifaceted systems into one value and should therefore be used in conjunction with other metrics to examine the health of the habitat as a whole.

I used traditional guilds – based on foraging, diet and nesting substrates – as well as total species richness as metrics in conjunction with the bird community index. There was overall general internal cohesion within guild functional groups, suggesting that responses of species within those groups were consistent (Figure 1). The majority of guilds and the total species richness however, had relatively weak correlations with the vegetation measures and did not show common trends (Table 1). In addition, designating priority levels for each metric is ambiguous, so no single guild could be weighted as more important than another.

Analysis of probability of occurrence versus canopy cover for the four top birds in each guild and habitat did not show consistent trends, indicating different responses toward canopy cover within the four grouped species (Figures 2 – 5). However, ten of the seventeen habitat assemblages and functional groups within guilds did show three species with similar responses to canopy cover and eight responses were generally expected. The decreased response of birds in the generalist assemblage, shrub nesters and ground foraging guilds can be explained because all are characteristically associated with habitats having decreased vegetation. Thus it is expected that probability of occurrence would decrease with increasing vegetation cover. Conversely, the increased response of the mature forest assemblage, canopy nesters, nectar feeders, seed feeders and flower foraging guilds can be explained because all are associated with habitats requiring vegetation and in the case of the mature forest assemblage, late successional vegetation.

It is therefore expected that the probability of occurrence for these species would increase with increasing vegetation cover.

In comparison to other studies, my results show much lower correlation values between species richness of functional groups and forest vegetation measures (Canterbury et al. 2000; Croonquist and Brooks 1991). This result could be explained due to the abundant number of bird species designated into the generalist assemblage. If the literature used to categorize the birds listed more than one preferred habitat for a species, that species was placed in the generalist habitat assemblage. This issue could be addressed using a more detailed definition, an additional habitat assemblage that takes into account or including the generalist category into the bird community index formula in order to provide for a more accurate classification system. Other factors that may have contributed to the low correlation values include potential sampling errors, guild classification errors and the weather conditions during which the sampling took place.

As a next step, I plan to include the conduct new analyses of the bird data after adjusting the bird community index formula to take into account the generalist assemblage. In terms of future applications, information from bird indices could be compiled with data from avian monitoring programs such as the Breeding Bird Survey and Christmas Bird Count. This would provide a broader pool of data to draw conclusions about patterns and trends from. Bird indices could also be applied to other ecosystems like wetlands and grasslands to assess potential influences on their respective status.

It would also be interesting to include the use of habitat vegetation to calculate a habitat index value for each site. Calculation of correlations between the bird community and habitat indices could be useful in determining the relationship between the two indices and if dependent, how well the habitat index could predict bird community index values. The habitat index could also be used to calculate variation in the bird community index. The degree of correlations between the habitat index and the vegetation measures (percent canopy cover and basal area) could be evaluated and compared to those of the bird community index to assess whether the habitat index has a stronger correlation.

Vegetation composition could be used as a measure to assess association to bird species diversity as well as a proxy of human disturbance on forests. In addition, data on land use and human population density could be included to assess the relationship between humans and forest condition since anthropogenic disturbances of forests often lead to loss of species that require undisturbed or late-successional conditions and species invasion which is indicated by dominance of species typical of early successional conditions (Mannan & Meslow 1984). This is important because species that require mature forest conditions may be particularly vulnerable to habitat loss and fragmentation.

Nevertheless, taking the above listed limitations into account, I argue that in regions of western Mexico where forest status data is not readily accessible, uncomplicated and time effective bird composition surveys can serve as a good tool for assessing forest condition. This information can contribute to long term monitoring programs in order to successfully evaluate population changes due to environmental conditions and to the management decision making process.

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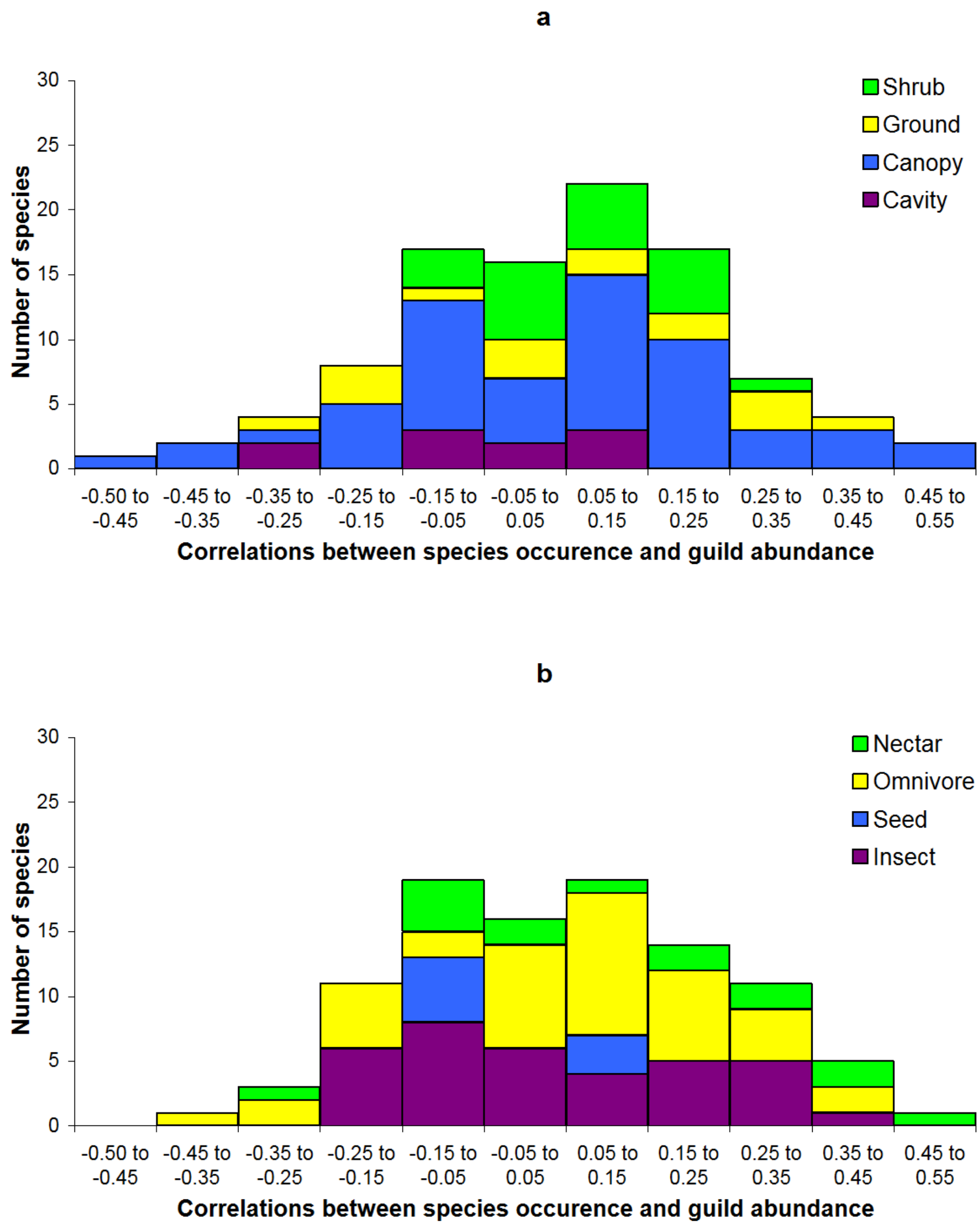
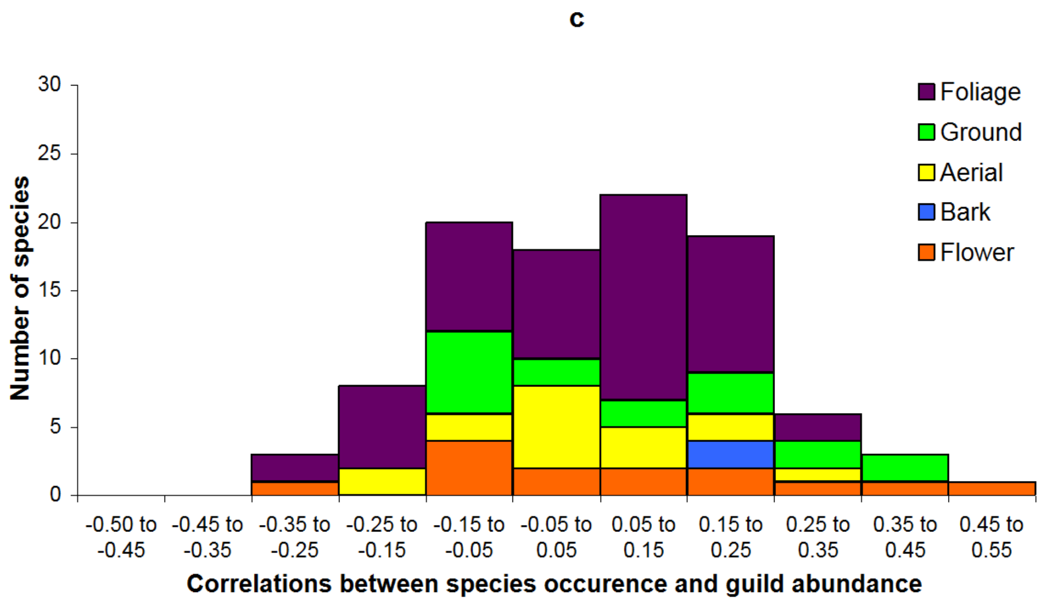


Figure 1. Correlations between presence or absence of individual bird species and the number of other bird species present from the same functional group for every individual species. Each datum shown in the histograms represents a species-group correlation coefficient for a single species. The four grouping criteria (Table 1) are plotted on different histograms: (a) nesting guilds, (b) diet guilds, (c) foraging guilds, (d) habitat assemblages. Plots with predominately positive correlations indicate functional groups that are internally cohesive with similar population responses in their constituent species. Single species groups are excluded.



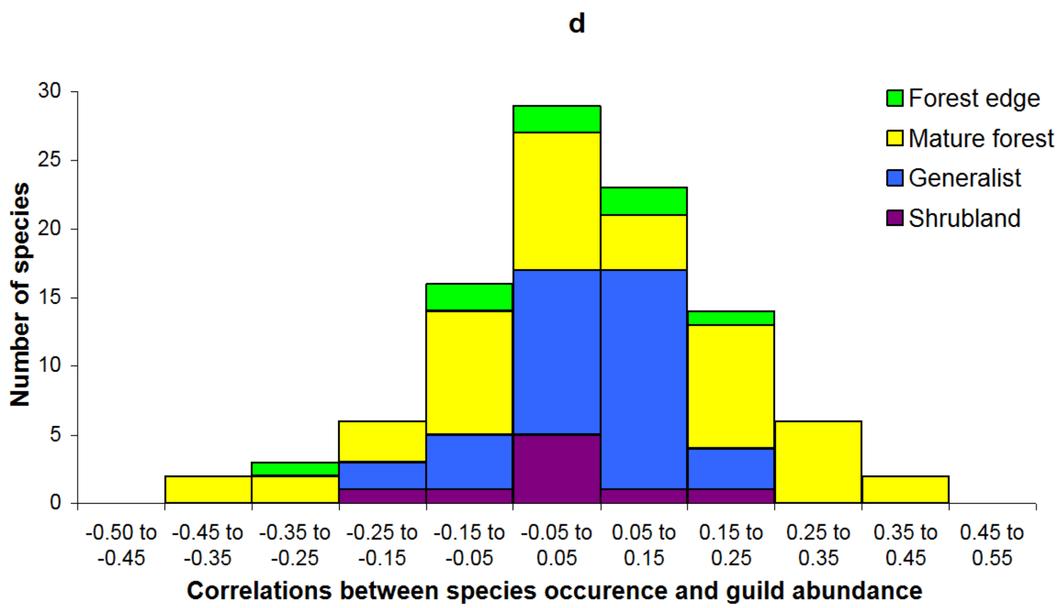


Figure 1 (continued). Correlations between presence or absence of individual bird species and the number of other bird species present from the same functional group for every individual species. Each datum shown in the histograms represents a species-group correlation coefficient for a single species. The four grouping criteria (Table 1) are plotted on different histograms: (a) nesting guilds, (b) diet guilds, (c) foraging guilds, (d) habitat assemblages. Plots with predominately positive correlations indicate functional groups that are internally cohesive with similar population responses in their constituent species. Single species groups are excluded.

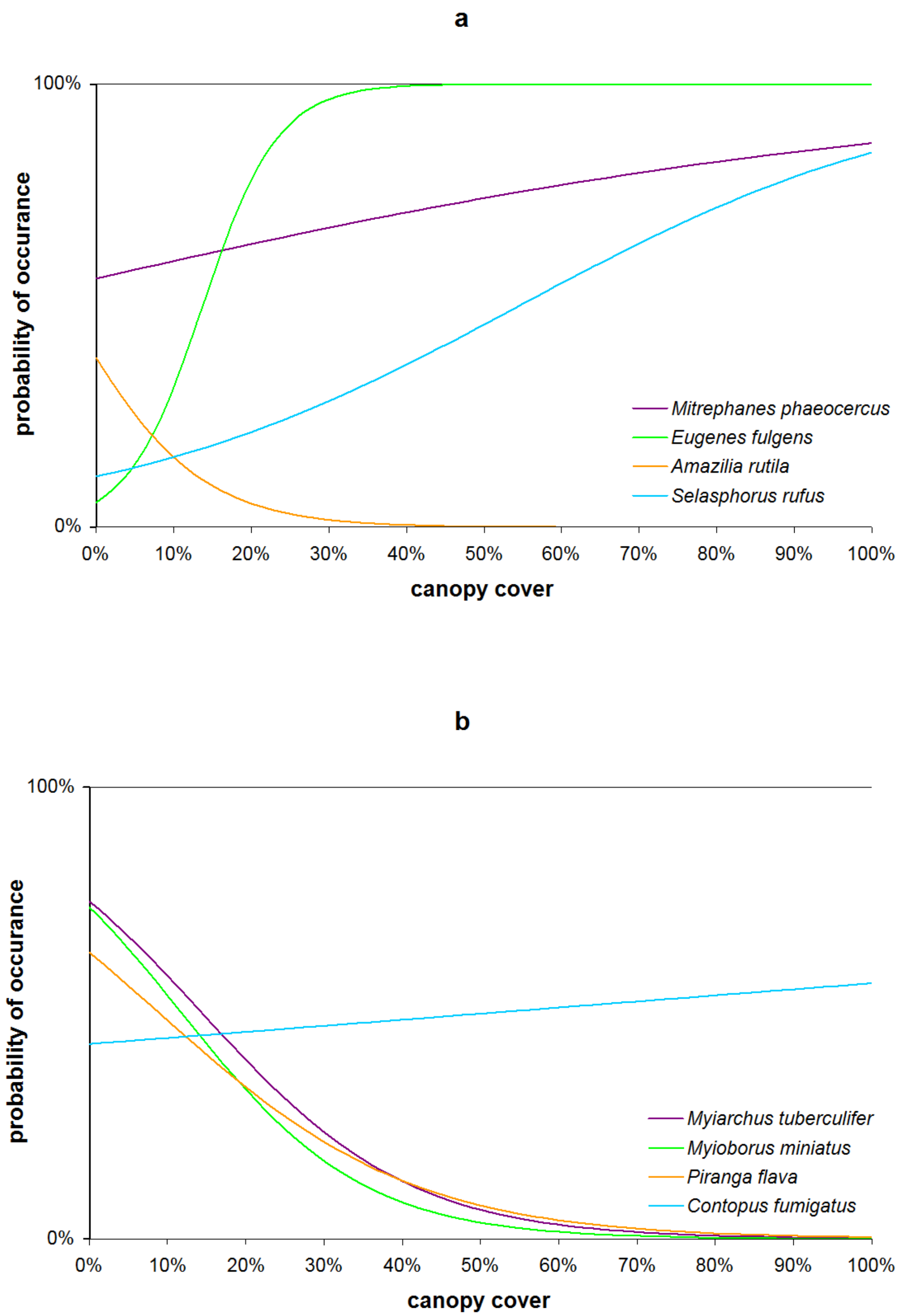
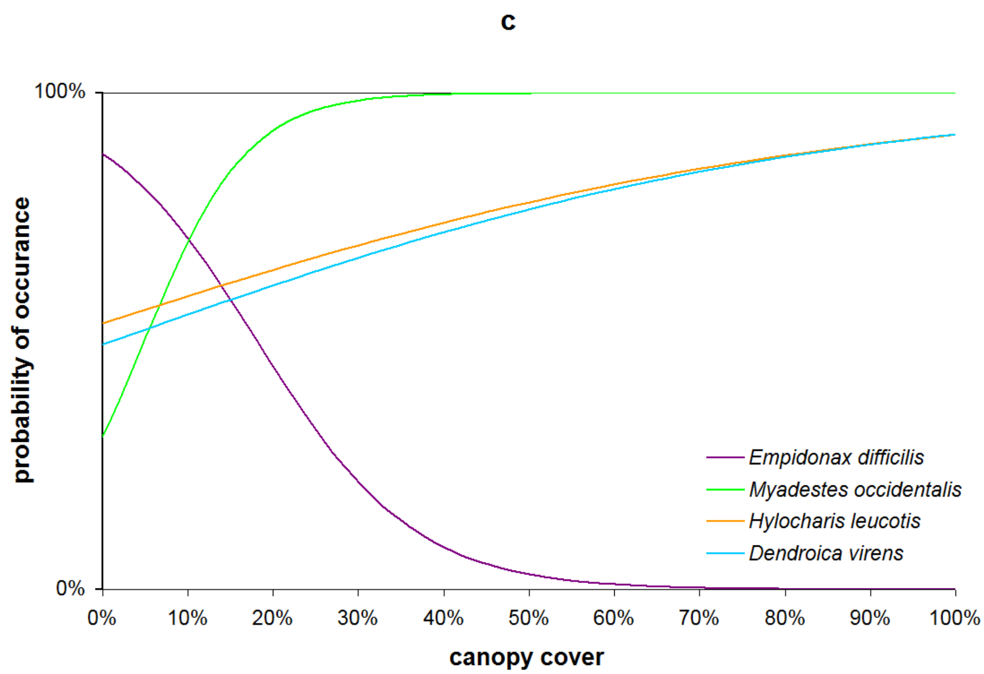


Figure 2. Probability of occurrence versus canopy cover for the four most abundant species in each of the four habitat assemblages: (a) forest edge, (b) generalist, (c) mature forest, (d) shrubland. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.



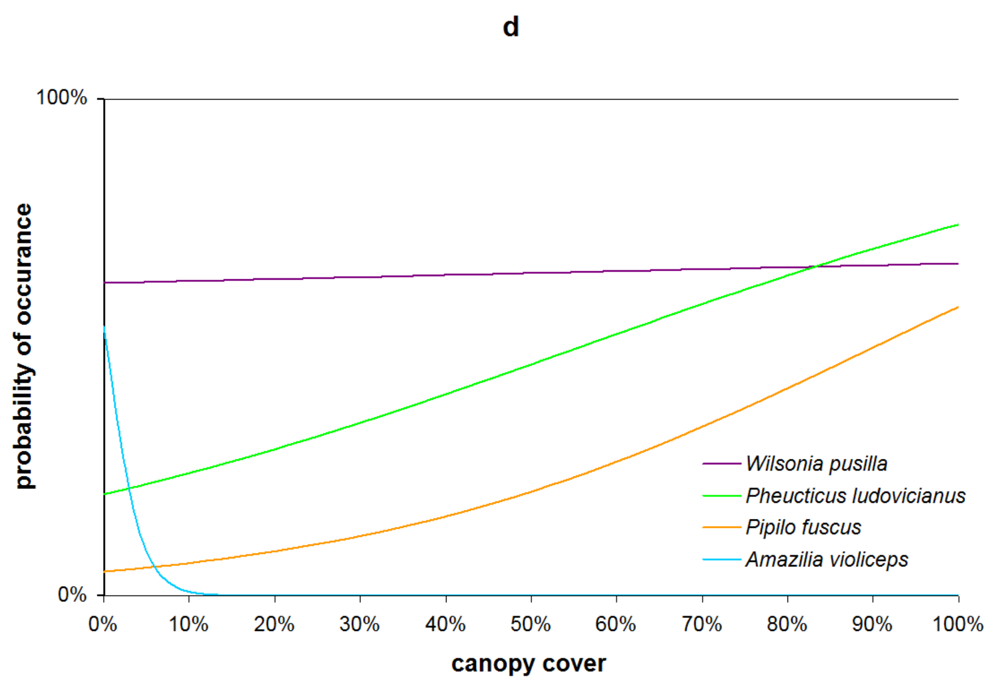
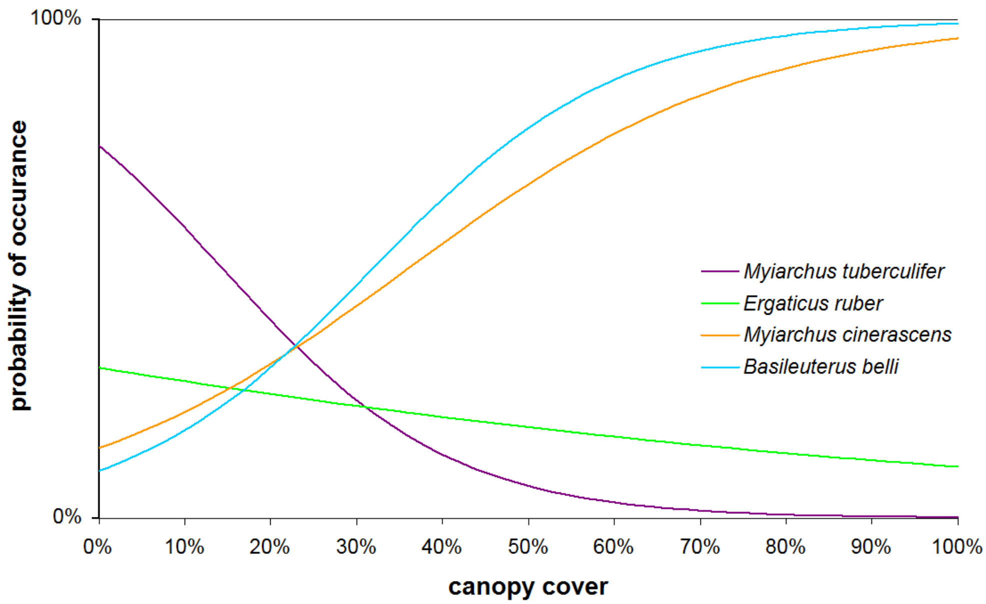


Figure 2 (continued). Probability of occurrence versus canopy cover for the four most abundant species in each of the four habitat assemblages: (a) forest edge, (b) generalist, (c) mature forest, (d) shrubland. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.

a



b

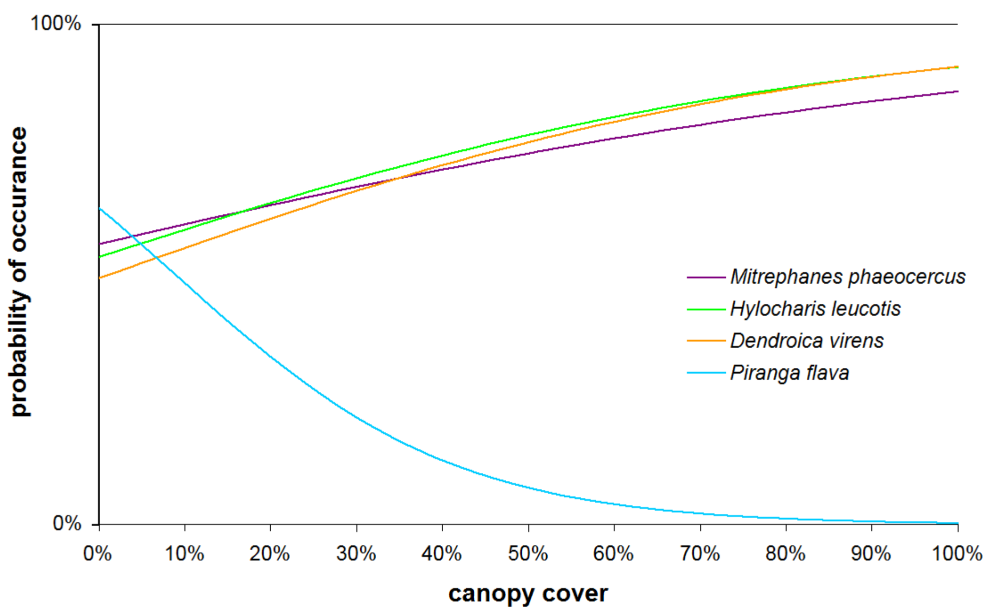
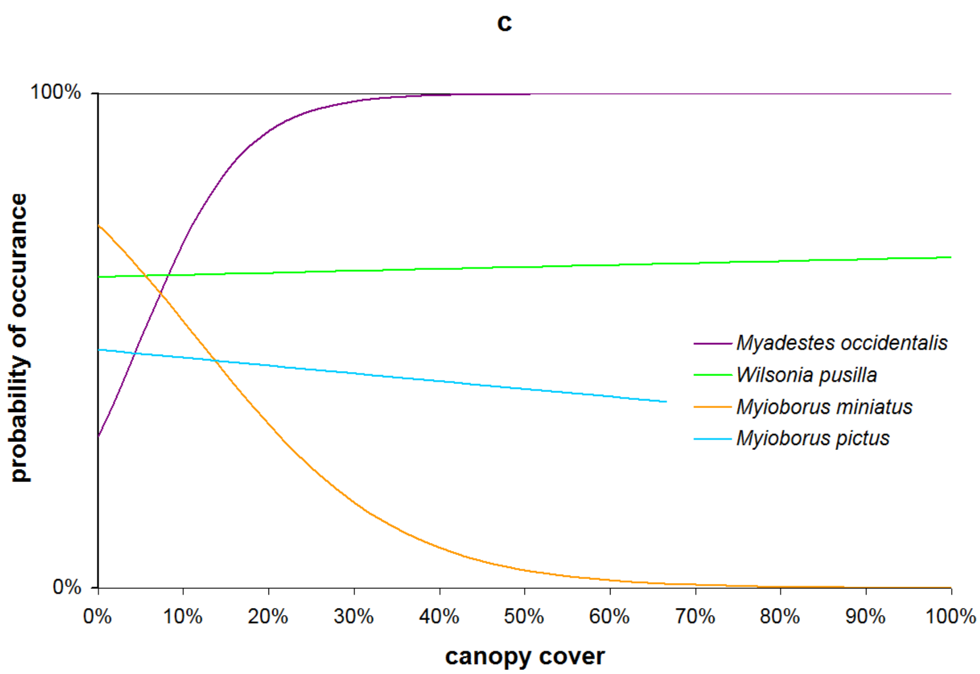


Figure 3. Probability of occurrence versus canopy for the four most abundant species in each of the four nesting guilds: (a) cavity nesting, (b) canopy nesting, (c) ground nesting, (d) shrub nesting. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.



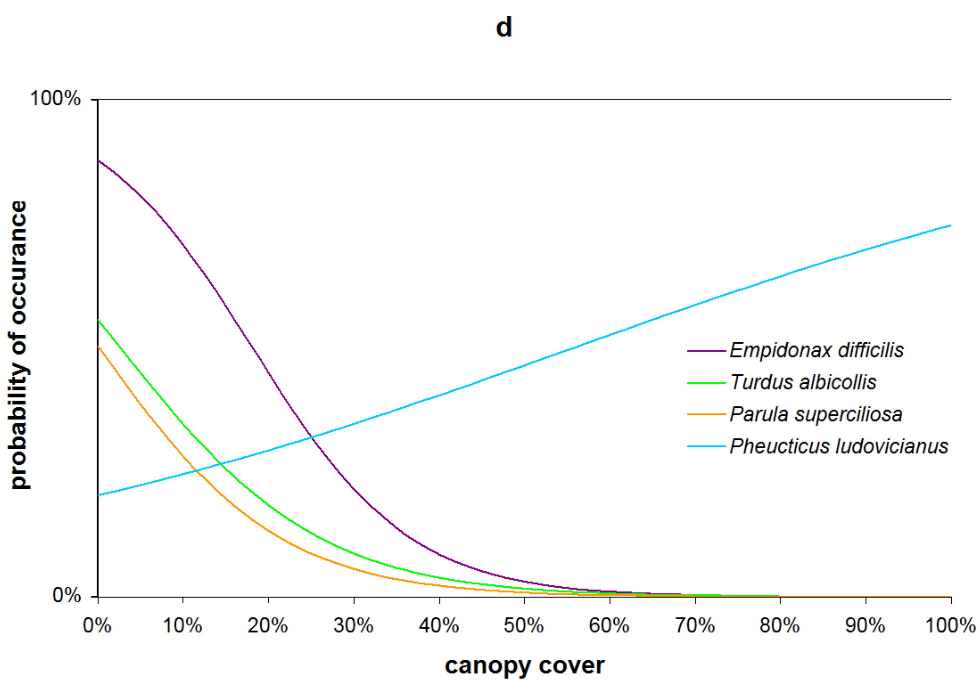


Figure 3 (continued). Probability of occurrence versus canopy for the four most abundant species in each of the four nesting guilds: (a) cavity nesting, (b) canopy nesting, (c) ground nesting, (d) shrub nesting. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.

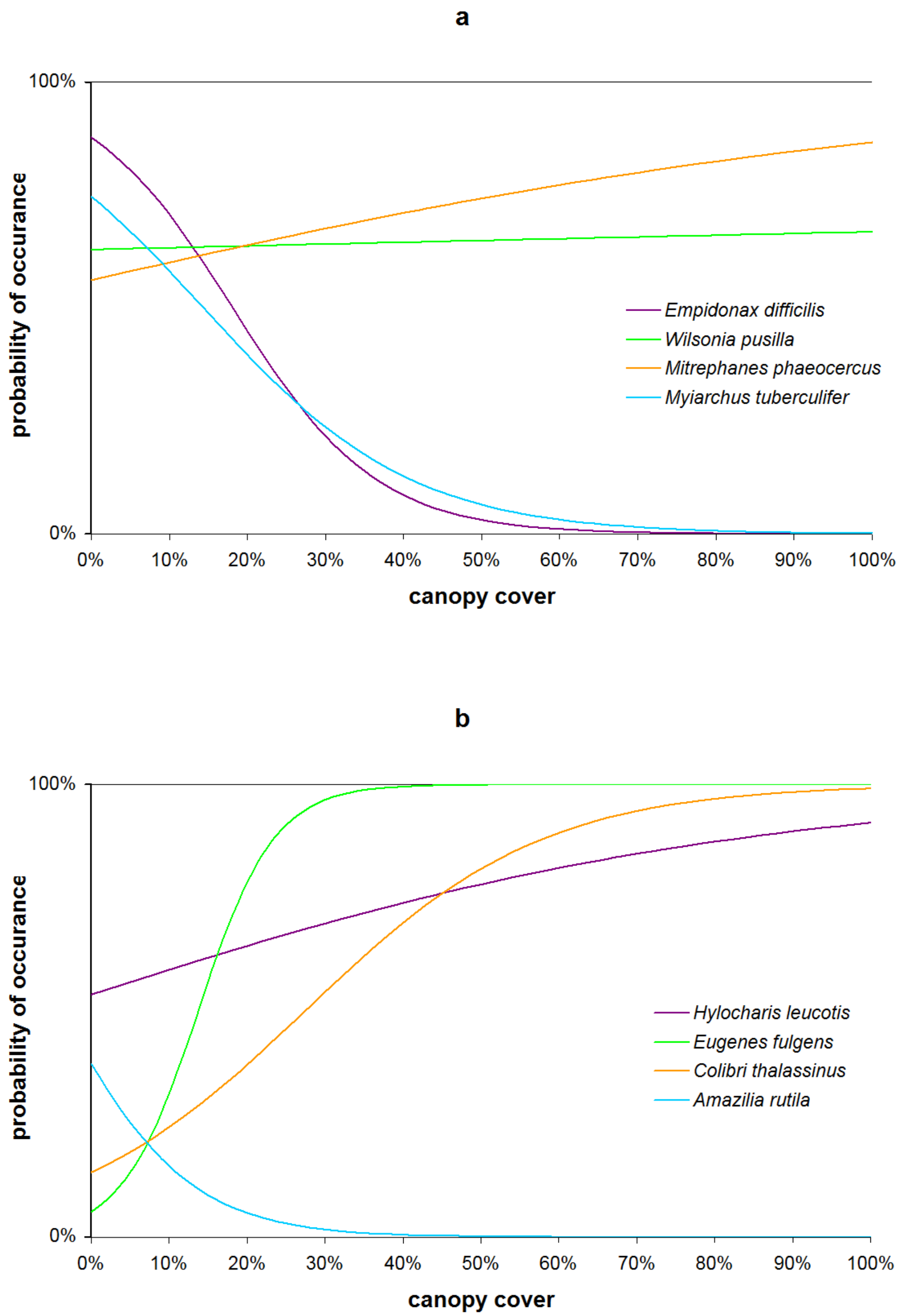
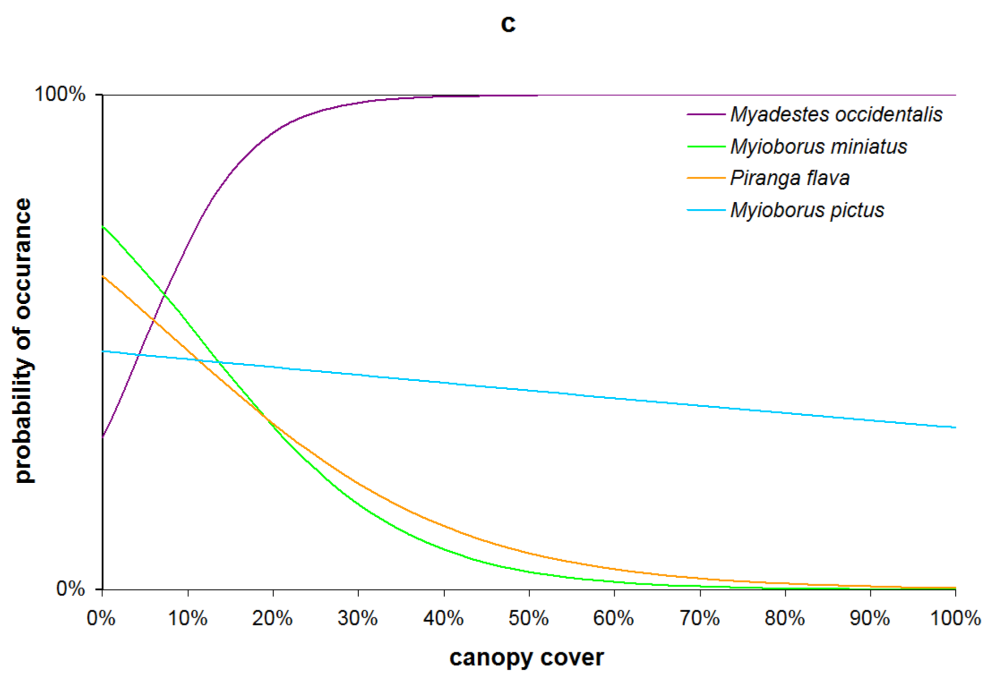


Figure 4. Probability of occurrence versus canopy for the four most abundant species in each of the four diet guilds: (a) insect feeding, (b) nectar feeding, (c) omnivores, (d) seed feeding. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.



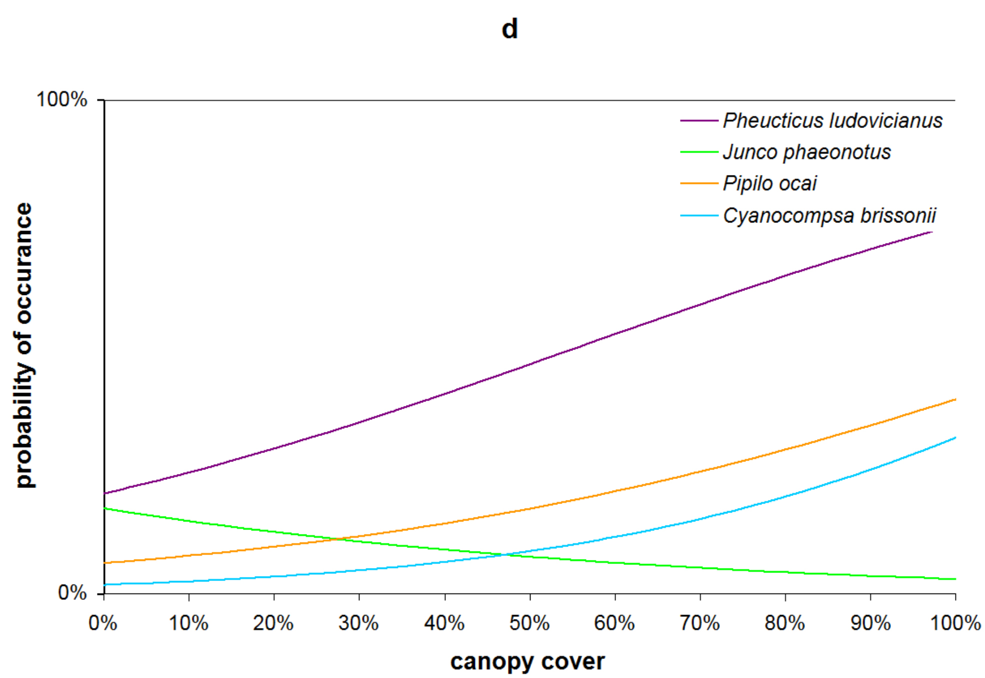


Figure 4 (continued). Probability of occurrence versus canopy for the four most abundant species in each of the four diet guilds: (a) insect feeding, (b) nectar feeding, (c) omnivores, (d) seed feeding. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.

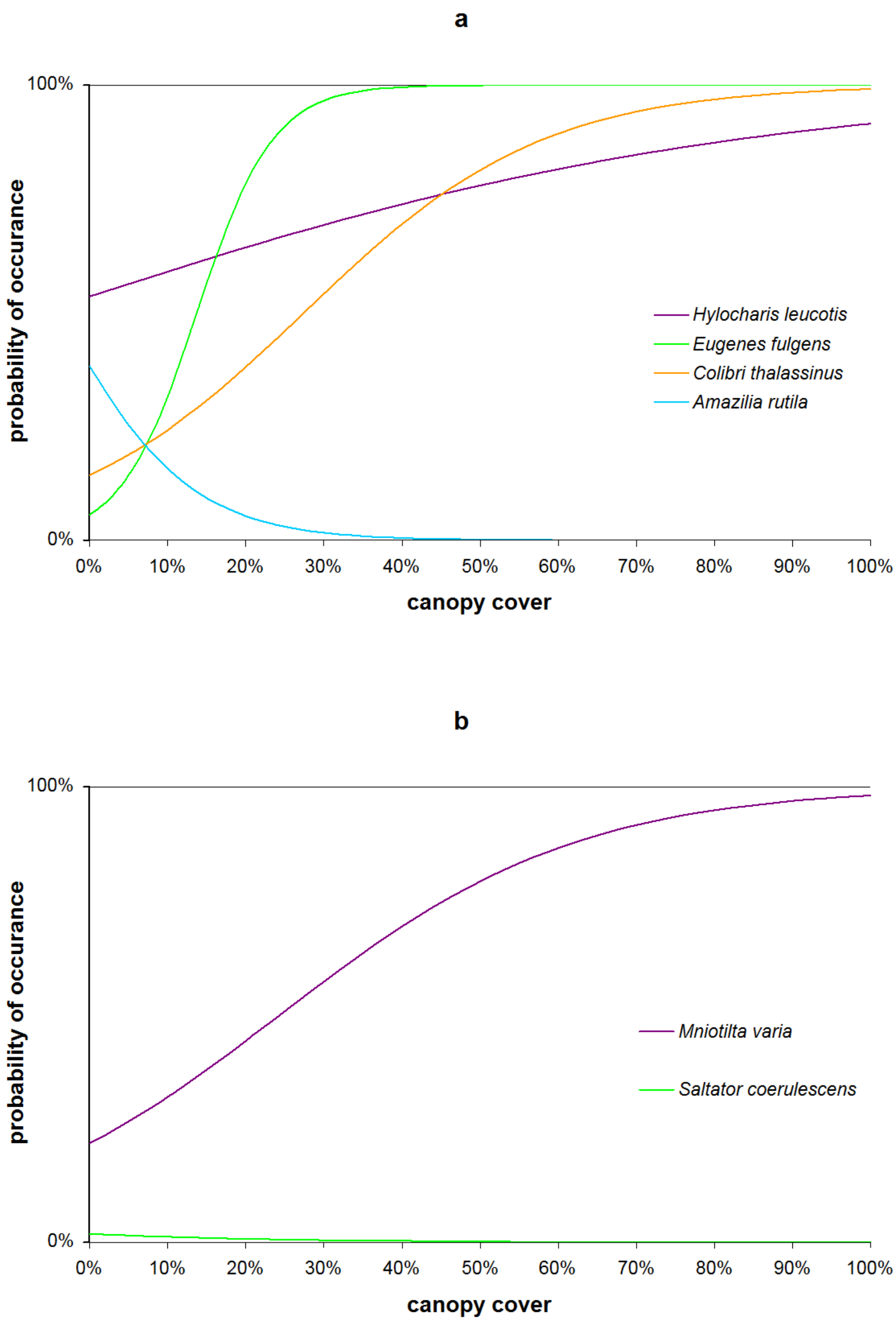
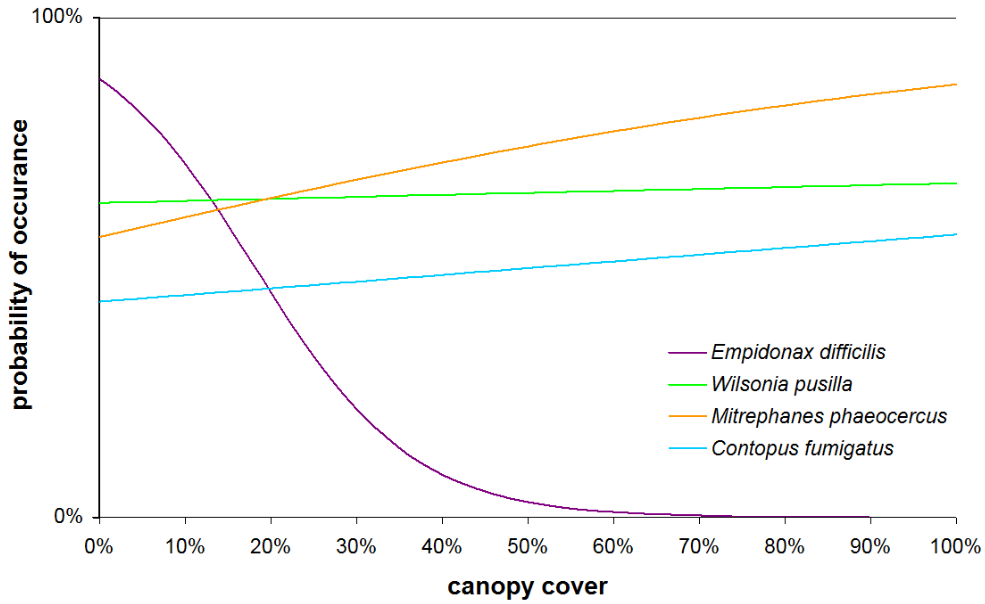


Figure 5. Probability of occurrence versus canopy for the four [x] *most abundant species in each of the five foraging guilds: (a) flower foraging, (b) bark foraging, (c) aerial foraging, (d) foliage foraging, (e) ground foraging. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.*

[*] *bark foraging guild contained two species only*

c



d

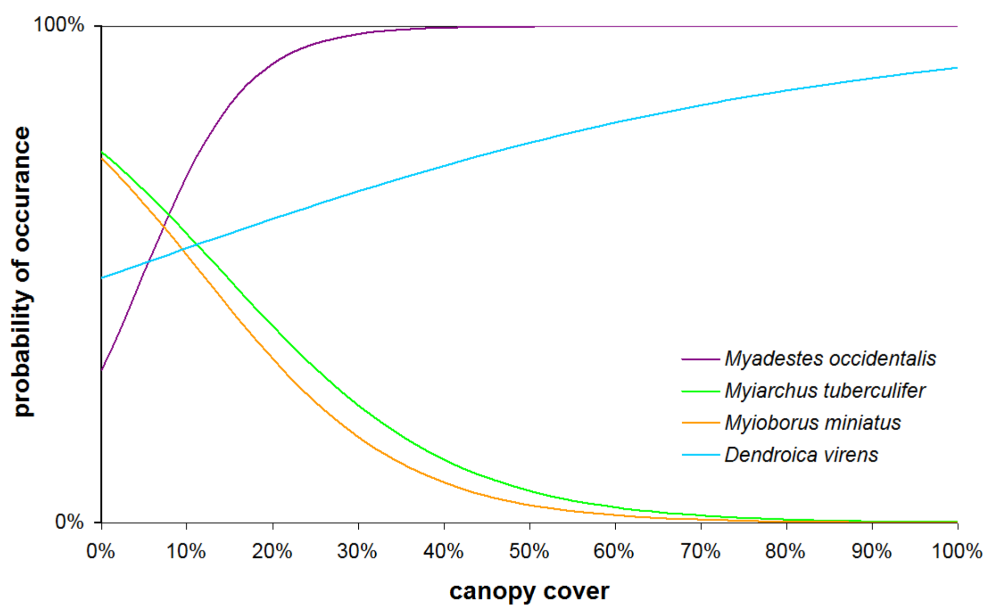


Figure 5 (continued). Probability of occurrence versus canopy for the four[x] most abundant species in each of the five foraging guilds: (a) flower foraging, (b) bark foraging, (c) aerial foraging, (d) foliage foraging, (e) ground foraging. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.

[*] *bark foraging guild contained two species only*

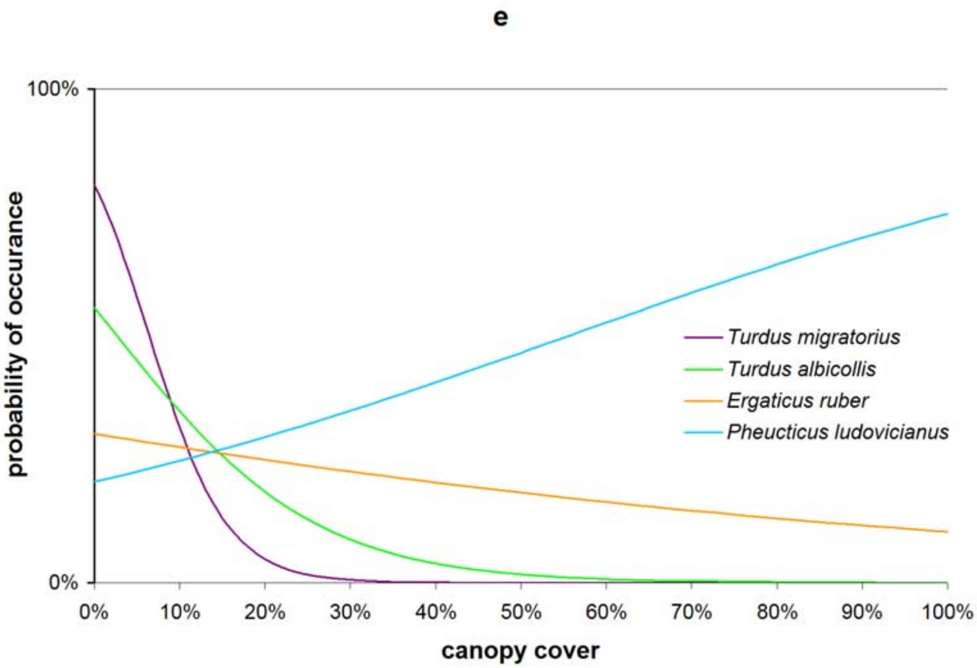


Figure 5 (continued). Probability of occurrence versus canopy for the four [x] most abundant species in each of the five foraging guilds: (a) flower foraging, (b) bark foraging, (c) aerial foraging, (d) foliage foraging, (e) ground foraging. Probabilities are calculated from binary logistic regression of species presence or absence versus canopy cover.

[*] *bark foraging guild contained two species only*

Table 1. Correlation coefficients relating bird community index and species richness of functional groups to percent canopy cover and basal area

Functional group classification	*Correlation* [a]	
	canopy cover	*tree basal area*
Diet guild		
Insectivores	-0.20	-0.06
Granivores/herbivores	-0.01	0.06
Omnivores	-0.06	-0.07
Nectarivores	0.14	-0.09
Foraging guild		
Flower-foraging	0.12	-0.11
Bark-foraging	0.09	0.12
Aerial-foraging	-0.12	-0.14
Ground-foraging	-0.10	0.05
Foliage-foraging	-0.14	-0.07
Nesting guild		
Ground nesters	0.07	0.04
Cavity nesters	-0.12	0.03
Canopy (tree branch) nesters	-0.02	-0.11
Shrub nesters	-0.26	-0.14
Habitat assemblage		
Forest edge species	0.16	-0.14
Shrubland species	-0.01	0.07
Generalist species	-0.19	-0.09
Mature forest species	-0.08	-0.06
Disturbance tolerant species (shrubland & forest edge)	0.11	-0.06
Bird community index [b]	-0.13	0.01
Total species richness	-0.10	-0.09

[a] *Probability: $p < 0.0001$*
[b] *Bird community index = $\ln(\text{mature forest} + 1) - \ln(\text{shrubland} + \text{forest edge} + 1)$*

Appendix 1

Names, abbreviated codes, membership in guilds and habitat assemblages, and abundance for bird species

Species name	*Code*	*Diet guild*	*Foraging guild*	*Nesting guild*	*# Points occupied*
Mature-forest assemblage					
Archilochus colubris Ruby-throated hummingbird	Arco	nectar	flowers	shrub	13
Atlapetes torquatus Stripe-headed brush finch	Atto	omnivore	foliage	shrub	10
Atthis heloisa Bumblebee hummingbird	Athe	insect	foliage	ground	9
Attila spadiceus Bright-rumped attila	Atsp	omnivore	ground	shrub	2
Basileuterus belli Golden-browed warbler	Babe	omnivore	foliage	cavity	13
Cardellina rubrifrons Red-faced warbler	Caru	omnivore	foliage	ground	17
Carduelis pinus Pine siskin	Capi	omnivore	foliage	canopy	2
Catharus frantzii Ruddy-capped nightingale-thrush	Cafr	omnivore	ground	shrub	5
Catharus guttatus Hermit thrush	Cagu	omnivore	ground	ground	7
Catharus occidentalis Russet nightingale-thrush	Caoc	omnivore	foliage	canopy	7
Catharus ustulatus Swainson's thrush	Caus	omnivore	foliage	canopy	3
Contopus borealis Olive-sided Flycatcher	Cobo	insect	aerial	canopy	1
Cynanthus latirostris Broad-billed hummingbird	Cyla	nectar	flowers	shrub	8
Dendroica coronata Yellow-rumped warbler	Deco	insect	aerial	canopy	25
Dendroica dominica Yellow-throated warbler	Dedo	insect	aerial	canopy	12
Dendroica nigrescens Black-throated grey warbler	Deni	insect	foliage	canopy	20
Dendroica virens Black-throated green warbler	Devi	insect	foliage	canopy	43
Empidonax difficilis Pacific-slope flycatcher	Emdi	insect	aerial	shrub	58
Empidonax fulvifrons Buff-breasted flycatcher	Emfu	insect	aerial	canopy	13
Ergaticus ruber Red warbler	Erru	insect	ground	cavity	22
Euphonia chrysopasta White-lored euphonia	Euch	omnivore	foliage	canopy	5
Euthlypis lachrymosa Fan-tailed warbler	Eula	insect	foliage	shrub	1
Habia rubica Red-crowned ant-tanager	Haru	omnivore	ground	canopy	1

(continued)

Appendix 1 (continued)

Species name	***Code***	***Diet guild***	***Foraging guild***	***Nesting guild***	***# Points occupied***
Hylocharis leucotis White-eared hummingbird	Hyle	nectar	flowers	canopy	46
Icterus galbula Baltimore oriole	Icga	omnivore	foliage	canopy	20
Icterus graduacauda Audubon's oriole	Icgr	omnivore	foliage	canopy	1
Icterus wagleri Black-vented oriole	Icwa	omnivore	foliage	canopy	1
Junco phaeonotus Yellow-eyed junco	Juph	seed	foliage	ground	12
Mniotilta varia Black-and-white warbler	Mnva	insect	bark	ground	24
Myadestes occidentalis Brown-baked solitaire	Myoc	omnivore	foliage	ground	50
Myioborus pictus Painted redstart	Mypi	omnivore	foliage	ground	37
Oporornis philadelphia Mourning warbler	Opph	insect	aerial	ground	4
Oriturus superciliosus Striped sparrow	Orsu	seed	ground	shrub	1
Pachyramphus major Grey-collared becard	Pama	insect	aerial	canopy	6
Pachyramphus minor Pink-throated becard	Pami	insect	aerial	canopy	3
Parula americana Northern parula	Paam	insect	foliage	canopy	3
Parula superciliosa Crescent-chested warbler	Pasu	insect	foliage	shrub	25
Peucedramus taeniatus Olive warbler	Peta	insect	foliage	canopy	17
Piranga ludoviciana Western tanager	Pilu	omnivore	foliage	canopy	19
Piranga rubra Summer tanager	Piru	insect	foliage	canopy	13
Sialia mexicana Western bluebird	Sime	omnivore	foliage	cavity	2
Stellula calliope Calliope hummingbird	Stca	insect	foliage	canopy	3
Turdus albicollis White-necked thrush	Tual	insect	ground	shrub	30
Turdus rufopalliatus Rufous-backed robin	Turu	omnivore	ground	canopy	3
Vermivora ruficapilla Nashville warbler	Veru	insect	foliage	ground	24
Zoothera pinicola Aztec thrush	Zopi	omnivore	foliage	canopy	2

(continued)

Appendix 1 (continued)

Species name	*Code*	*Diet guild*	*Foraging guild*	*Nesting guild*	*# Points occupied*
Shrubland assemblage					
Aimophila ruficeps Rufous-crowned sparrow	Airu	seed	ground	ground	1
Amazilia violiceps Violet-crowned hummingbird	Amvi	nectar	flowers	shrub	3
Passerina ciris Painted bunting	Paci	insect	ground	shrub	1
Passerina versicolor Varied bunting	Pave	seed	ground	canopy	1
Pheucticus chrysopeplus Yellow grosbeak	Phch	seed	ground	shrub	1
Pheucticus ludovicianus Rose-breasted grosbeak	Phlu	seed	ground	shrub	19
Pipilo fuscus Canyon towhee	Pifu	insect	ground	canopy	5
Tyrannus vociferans Cassin's kingbird	Tyvo	insect	aerial	canopy	1
Wilsonia pusilla Wilson's warbler	Wipu	insect	aerial	ground	51
Forest-edge assemblage					
Amazilia beryllina Berylline hummingbird	Ambe	nectar	flowers	shrub	11
Amazilia rutila Cinnamon hummingbird	Amru	nectar	flowers	shrub	15
Basileuterus rufifrons Rufous-capped warbler	Baru	omnivore	foliage	cavity	11
Catharus aurantiirostris Orange-billed nightingale-thrush	Caau	omnivore	ground	canopy	7
Eugenes fulgens Magnificient hummingbird	Eufu	nectar	flowers	canopy	21
Mitrephanes phaeocercus Tufted flycatcher	Miph	insect	aerial	canopy	47
Selasphorus rufus Rufous hummingbird	Seru	nectar	flowers	shrub	12
Tityra semifasciata Masked tityra	Tise	omnivore	foliage	cavity	12
Tyrannus crassirostris Thick-billed kingbird	Tycr	insect	aerial	canopy	4
Habitat generalist assemblage					
Atlapetes pileatus Rufous-capped brush-finch	Atpi	omnivore	foliage	shrub	2
Cacicus melanicterus Yellow-winged cacique	Came	omnivore	foliage	canopy	11
Camptostoma obsoletum Southern-beardless-tyrannulet	Caob	omnivore	ground	canopy	1
Cardinalis cardinalis Northern cardinal	Caca	omnivore	foliage	shrub	1

(continued)

Appendix 1 (continued)

Species name	***Code***	***Diet guild***	***Foraging guild***	***Nesting guild***	***# Points occupied***
Chlorostilbon aureoventris Glittering-bellied emerald	Chau	nectar	flowers	shrub	2
Colibri thalassinus Green violet-ear	Coth	nectar	flowers	canopy	18
Contopus fumigatus Smoke-colored pewee	Cofu	insect	aerial	canopy	35
Cyanocompsa brissonii Ultramarine grosbeak	Cybr	seed	foliage	canopy	2
Diglossa baritula Cinnamon-bellied flower-piercer	Diba	nectar	foliage	canopy	4
Euphonia musica Antillean euphonia	Eumu	omnivore	foliage	cavity	6
Heliomaster constantii Plain-capped starthroat	Heco	nectar	flowers	canopy	1
Icterus cucullatus Hodded oriole	Iccu	omnivore	foliage	canopy	10
Icterus parisorum Scott's oriole	Icpa	omnivore	foliage	canopy	3
Icterus pectoralis Spot-breasted oriole	Icpe	omnivore	foliage	canopy	1
Icterus spurius Orchard oriole	Icsp	omnivore	foliage	canopy	1
Lampornis clemenciae Blue-throated hummingbird	Lacl	nectar	flowers	canopy	5
Megarhynchus pitangua Boat-billed Flycatcher	Mepi	insect	aerial	canopy	1
Myiarchus cinerascens Ash-throated flycatcher	Myci	insect	foliage	cavity	16
Myiarchus tuberculifer Dusky-capped flycatcher	Mytu	insect	foliage	cavity	48
Myiarchus tyrannulus Brown-crested flycatcher	Myty	insect	foliage	cavity	13
Myioborus miniatus Slate-throated redstart	Mymi	omnivore	foliage	ground	45
Myiopagis viridicata Greenish elaenia	Myvi	omnivore	foliage	canopy	1
Myiozetetes similis Sociel flycatcher	Mysi	insect	aerial	canopy	5
Passerina leclancherii Orange-breasted bunting	Pale	seed	foliage	shrub	1
Pipilo erythrophthalmus Rufous-sided towhee	Pier	omnivore	ground	ground	19
Pipilo ocai Collared towhee	Pioc	seed	ground	ground	6
Piranga bidentata Flame-colored tanager	Pibi	omnivore	foliage	canopy	3

(continued)

Appendix 1 (continued)

Species name	*Code*	*Diet guild*	*Foraging guild*	*Nesting guild*	*# Points occupied*
Piranga flava Hepatic tanager	Pifl	omnivore	foliage	canopy	40
Pitangus sulphuratus Great kiskadee	Pisu	omnivore	foliage	building	11
Saltator coerulescens Greyish saltator	Saco	omnivore	bark	canopy	1
Selasphorus platycercus Broad-tailed hummingbird	Sepl	nectar	flowers	canopy	10
Sialia sialis Eastern bluebird	Sisi	insect	foliage	cavity	9
Spizella pallida Clay-colored sparrow	Sppa	omnivore	ground	ground	1
Spizella passerina Chipping sparrow	Spps	omnivore	ground	canopy	1
Tilmatura dupontii Sparkling-tailed hummingbird	Tidu	nectar	flowers	shrub	1
Turdus migratorius American robin	Tumi	omnivore	ground	canopy	32
Vermivora celata Orange-crowned warbler	Vece	omnivore	foliage	ground	18